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TECHNICAL REPORT NO. 25

BREEDING ECOLOGY OF RIPARIAN BIRDS ALONG THE COLORADO RIVER IN GRAND CANYON, ARIZONA

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COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT
University of Arizona/Tucson - National Park Service

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ECOLOGY OF RIPARIAN BREEDING BIRDS
ALONG THE COLORADO RIVER IN GRAND CANYON, ARIZONA

by

Bryan Turner Brown

A Dissertation Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES DIVISION
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ABSTRACT

The density, diversity, and nest-site selection of riparian breeding birds were studied from 1982 to 1985 in mesquite (*Prosopis glandulosa*) and tamarisk (*Tamarix chinensis*) communites along the Colorado River in northern Arizona. Avian density in tamarisk communities was significantly greater than avian density in native mesquite communities with similar vegetative cover and height attributes. Avian diversity was similar in both habitats. Breeding bird densities in tamarisk were higher than those reported from other geographic areas.

Vegetation structure and shrub species composition were measured at nest sites of eleven species of riparian birds in a tamarisk community to examine avian habitat relationships. Riparian birds exhibited differences in their choice of nesting habitat. Discriminant analysis indicated that Bell's Vireo (*Vireo bellii*) and Willow Flycatcher (*Empidonax traillii*) were generalists in nest site selection, while American Coot (*Fulica americana*) and Blue Grosbeak (Guiraca caerulea) were habitat specialists. Bell's Vireo and American Coot used the most dissimilar habitats. Willow Flycatcher and Yellow Warbler (*Dendroica petechia*) used the most similar habitats. Willow Flycatcher and Yellow Warbler consistently used habitat most similar to that used by all other species.

Nest placement preferences of six riparian passerines were examined in a tamarisk-dominated community to test the null hypothesis that nest placement in any given species of shrub was random. Ninety-five of 105 nests sampled were located in tamarisk as opposed to native shrubs. Five of the six species of passerines exhibited a significant preference for tamarisk for nest placement. A highly significant preference for tamarisk was shown by the four species with the smallest median frequency of tamarisk in their nesting habitat. The usefulness of tamarisk for nest placement was higher than that reported from other areas.

CHAPTER 1

INTRODUCTION

Native riparian communities support the highest known breeding densities of non-colonial land birds in North America (Carothers et al., 1974; Willet and Van Velzen, 1984). These productive communities provide essential nesting habitat for many species of birds in the Southwest. Many of these species are entirely dependent on riparian habitat in which to breed (Johnson et al., 1977) and do not nest elsewhere. Nevertheless, avian habitat selection and nest-site selection in riparian habitats is only partly understood, especially in riparian habitats dominated by tamarisk (*Tamarix chinensis*).

Tamarisk is a widespread, introduced shrub of low-elevation riparian areas in the Southwest, where it dominates over 100,000 ha of streamside habitat (Horton, 1977). Avian breeding ecology in tamarisk communities has only been studied extensively along the Lower Colorado River (Hunter et al., 1985) where tamarisk occurs in a different growth form than on the Upper Colorado River. Studies on avian nesting use of tamarisk along the Upper Colorado River are needed to determine if avian density, community organization, and habitat selection there are substantially different from that seen along the Lower Colorado River where early management guidelines on the value of tamarisk habitat to breeding birds were developed. If avian breeding use of tamarisk between the two regions is different, then unique guidelines would need to be developed for the management of breeding bird habitat along the Upper Colorado River.

I chose the riparian corridor of the Upper Colorado River through Grand Canyon in which to examine avian breeding ecology in tamarisk. The Colorado River in this setting provided extensive tamarisk-dominated communities, as well as mesquite (*Prosopis glandulosa*)-dominated communities. The purpose of this study was to determine if avian nesting use of tamarisk in the Grand Canyon differed from that observed in other areas and to identify patterns of habitat selection and nest-site selection in obligate riparian breeding birds. The study had three main objectives. Each objective was designed to explore in progressively finer detail the nesting behavior of birds in tamarisk communities.

The first objective had several components. These were 1) to document the density and diversity of breeding birds in both tamarisk and mesquite communities; 2) to compare avian breeding use of Grand Canyon riparian communities with that observed in other areas; 3) to compare avian density between mesquite and

tamarisk communities in the Grand Canyon to see which was more productive for birds; and 4) to analyze structural differences in the vegetation to determine if vegetation differences accounted for differences in avian community organization and density. This was done because it was necessary to first document the existing bird community in tamarisk, and to compare it to adjacent native habitats and other geographic areas, before proceeding to any more detailed analysis of avian nesting use of tamarisk.

The second objective was to examine nesting habitat differences between species of obligate riparian breeding birds in tamarisk. This was done to determine if obligate riparian birds showed a strong preference for different vegetation structures within the tamarisk community.

And finally, the third objective was to examine the nest placement preferences of selected obligate riparian birds in tamarisk to determine if tamarisk was preferred over native plants as a nest site. This was done because it was necessary to determine, after first determining the density and habitat preferences of birds nesting in tamarisk, whether or not the availability of native plants was a limiting factor in determining avian density and habitat preferences. If tamarisk was preferred over native plants as a nest site, this would help to explain why breeding birds could occur in such high densities in tamarisk and why such diverse patterns of habitat selection were observed in tamarisk-dominated communities.

CHAPTER 2

BREEDING BIRDS OF MESQUITE AND TAMARISK COMMUNITIES

Introduction

Woodlands of mesquite or tamarisk are among the most abundant vegetative communities available to low-elevation riparian breeding birds in the southwestern United States (Hunter et al., 1985). The importance of mesquite habitat to southwestern riparian breeding birds has been widely established (Austin, 1970; Carothers et al., 1974; Gavin and Sowls, 1975; Stamp, 1978). Studies from the Lower Colorado River (Anderson et al, 1977; Cohan et al, 1978) showed tamarisk, an introduced species, to be of mixed importance to riparian breeding birds. However, Hunter et al. (1985) found that breeding bird use of tamarisk varied between three southwestern river systems: the Lower Colorado, Pecos, and Rio Grande. Their findings indicated low avian use of tamarisk on the Lower Colorado River, while the proportion of bird populations using tamarisk on the Pecos River was as high or higher in most cases than the proportion of bird populations using native riparian habitats. Hunter et al. (1985) suggested these differences in avian use of tamarisk were due to biogeographic and climatic factors. If avian use of tamarisk is subject to biogeographic variation, then regional strategies for the management of tamarisk as avian habitat need to be developed in order to properly manage tamarisk habitats for breeding birds under different conditions.

I studied the density and diversity of breeding birds in mesquite and tamarisk-dominated communities along the Colorado River in northern Arizona. My objectives were to document the density and diversity of breeding birds in the two community types, to compare avian use of the two communities to see which was more valuable to birds, and to analyze structural differences in the vegetation in order to determine if vegetative structure affected avian community composition. This information would make it possible to determine if avian breeding use of tamarisk in northern Arizona differed sufficiently from that reported from other geographic areas to warrant a unique regional management strategy.

Study Area

Ten sets of paired study sites (Table 1) were established along the Colorado River between Glen Canyon Dam and Diamond Creek, a distance of 389 km by river. All study sites were within the

boundaries of Glen Canyon National Recreation Area or Grand Canyon National Park, Arizona. The paired study sites (one each in mesquite and tamarisk habitats) were located in the largest and most well-developed stands of riparian vegetation present in each of the ten river reaches sampled. River reaches were selected to represent the entire spectrum of habitat sizes. and types present throughout the study area. Study sites were linear, narrow strips of vegetation at or near the water's edge. Site boundaries were noted on detailed aerial photographs, from which the area of each site was calculated with an electronic digital planimeter.

The completion of Glen Canyon Dam in 1963 had a major influence on the distribution of riparian vegetation in the study area. Prior to construction of the dam, the old-high-water-zone vegetation existed as a narrow band above the predam scour zone. This vegetative zone was dominated by honey mesquite; common associated vegetation included catclaw acacia (*Acacia greggii*), netleaf hackberry (*Celtis reticulata*), Apache plume (*Fallugia paradoxa*), redbud (*Cercis canadensis*), and scrub oak (*Quercus turbinella*).

Completion of the dam curtailed annual floods on the river and allowed the development of a new-high-water-zone of vegetation in the predam scour zone which was formerly devoid of vegetation (Turner and Karpiscak, 1980). This vegetative zone was dominated by tamarisk; associated vegetation included coyote willow (*Salix exigua*), Goodding willow (*Salix gooddingii*), arrowweed (*Tessaria sericea*), seepwillow (*Baccharis* spp.), and reed (*Phragmites australis*).

The tamarisk habitats (closest to the water) and the relict mesquite habitats (farthest from the water) together formed adjacent, linear belts of discontinuous riparian vegetation of up to 150 m in total width. Although quantitative data are lacking, approximately 300-500 ha of riparian vegetation were present along the river in 1982, of which approximately three-fourths was tamarisk-dominated with the remaining one-fourth dominated by mesquite.

Methods

Percent canopy cover and maximum vegetation height were measured in April 1984 along 60 m of random line-intercept vegetation transects in each study site (Canfield, 1941). The total distance of transect length covered by living vegetation of each species was added together (resulting in totals often exceeding 100%) and divided by 60 to generate percent canopy cover values for each site. Maximum vegetation height was measured to the nearest 0.5 m with a telescoping height pole at 15 predetermined points along each 60 m of transect length.

Table 1. Location and size of mesquite-dominated (-A) and tamarisk-dominated (-B) study sites along the Colorado River in Grand Canyon.

Site No.	Location	River Mile*	Elevation (m)	Area (ha)
01-A	Glen Canyon	7.4L**	960	1.7
01-B	Lees Ferry	0.3R**	945	2.9
02-A	Saddle Canyon	47.0R	855	1.6
02-B	Saddle Canyon	46.5R	855	2.8
03-A	Cardenas Creek	70.8L	800	1.5
03-B	Cardenas Marsh	71.0L	800	1.7
04-A	Lower Bass Camp	108.6R	670	0.1
04-B	Lower Bass Camp	108.6R	670	0.1
05-A	Forster Canyon	122.8L	635	0.6
05-B	Forster Canyon	122.7L	635	0.4
06-A	National Canyon	166.8L	535	2.2
06-B	National Canyon	166.3L	535	0.4
07-A	Stairway Canyon	170.8R	525	1.7
07-B	Stairway Canyon	171.0R	525	0.7
08-A	Parashant Canyon	198.2R	465	1.4
08-B	Parashant Canyon	198.0R	465	0.5
09-A	Granite Park	208.6L	440	5.6
09-B	Granite Park	208.7L	440	1.0
10-A	220-Mile Canyon	219.9R	420	0.9
10-B	Granite Spring Canyon	220.3L	420	0.1

*R and L refer to river right and river left, respectively, as one looks downstream. River Miles were place names taken from Stevens (1983).

**River Miles upstream of River Mile 0 at Lees Ferry. All remaining River Miles are downstream of Lees Ferry.

Breeding birds were censused by means of the direct count method (Emlen, 1971). The discrete, linear nature of the small study sites, which were in effect island habitats, made possible a virtually complete count of breeding birds. All birds seen or heard at each study site were recorded during three to five censuses in the spring and early summer of 1984 and again in 1985. Census periods were: 10 April to 1 July 1984 and 20 April to 18 June 1985. Censuses were conducted between 0500 and 1030 hours and 1745 and 1930 hours. The maximum number of pairs detected in any count for a site was used as the final number of breeding pairs. However, House Finches (*Carpodacus mexicanus*) were censused only in April and early May during their peak of breeding and before large numbers of House Finches were attracted to the river from other areas in order to obtain drinking water. Likewise, Yellow Warblers (*Dendroica petechia*) were censused in late May and June after most migrant Yellow Warblers had already moved through.

A 1:1 sex ratio was assumed for all breeders, in spite of the fact that sex ratios of some species may vary or fluctuate throughout the season (Mayfield, 1981). An exception was the density of Brown-headed Cowbirds (*Molothrus ater*), which was based on the number of females present (Stamp, 1978). If only one or more males were present or cowbird eggs or young were detected, then a value of one pair of Brown-headed Cowbirds was assigned to the site. Densities of Costa's Hummingbirds (*Calypte costae*) were based on the number of displaying males present. Black-chinned Hummingbird (*Archilochus alexandri*) densities were based on either the number of active nests discovered (Stamp, 1978) or, if no nests were found or the number of females observed exceeded the number of nests found, the number of females observed. These techniques probably underestimated the true hummingbird density.

Intensive nest searches were conducted by up to six skilled observers at each study site after a census. Nest searches provided supplemental information on secretive species, indicated more accurately the nesting density of species with unequal sex ratios, and provided insight into the degree of accuracy of the censuses. The discovery of an active nest of a species overlooked in the census was treated as a pair of birds in the final analysis. Small study sites were searched completely, while representative samples of larger sites were searched. The territory or extent of activity of a breeding pair was found to be only partly within the study sites in a few instances. When this occurred, arbitrary values of 0.5 pair were assigned for partial use (approximately half or less of a pair's activity) and 0.25 pair for occasional use (approximately a quarter or less of a pair's activity).

Bird species diversity was calculated by the formula:

$$H' = - \text{sum} [p_i \log p_i]$$

where p is the proportion of all the bird individuals which belong to i, or each of the species of birds present (MacArthur and MacArthur, 1961).

Results

The mesquite-dominated study sites exhibited two to 14 species in 1984, and three to 17 species in 1985 (See Tables 2 and 3). Densities in mesquite habitats ranged from 182 to 986 pairs/40 ha in 1984, and from 73 to 943 pairs/40 ha in 1985. Black-chinned Hummingbird, Ash-throated Flycatcher (*Myiarchus cinerascens*), Blue-gray Gnatcatcher (*Polioptila caerulea*), and Lucy's Warbler (*Vermivora luciae*) occurred most consistently in mesquite study sites. For example, these four ubiquitous species comprised 56.5% of the total density and 40% of total species in 1985 at the well-developed Cardenas Wash site (3-A). Mourning Dove (*Zenaida macroura*) and House Finch were each widespread for one of the two years of study. Lucy's Warbler was consistently the most abundant and widespread breeding bird in mesquite habitats in both 1984 and 1985.

Tamarisk-dominated sites exhibited one to 15 species in 1984, and one to 16 species in 1985 (See Tables 4 and 5). Densities in tamarisk varied from 200 to 1200 pairs/40 ha in 1984, and from 100 to 1200 pairs/40 ha in 1985. Black-chinned Hummingbird, Blue-gray Gnatcatcher, Lucy's Warbler, Yellow Warbler, and Common Yellowthroat (*Geothlypis trichas*) occurred most consistently in tamarisk habitats. These five widespread NHWZ species comprised 51.5% of the total density and 31% of the total species in 1985 at the well-developed Cardenas Marsh site (3-B). Lucy's Warbler and Black-chinned Hummingbird were the most abundant and widespread species in tamarisk habitats during both years.

The mean density of breeding birds in tamarisk habitats was greater than that of mesquite habitats. Mean avian density in tamarisk was 610.5 pairs/40 ha in 1984 and 565.2 pairs/40 ha in 1985; mean avian density in mesquite was 449.3 pairs/40 ha in 1984 and 378.7 pairs/40 ha in 1985. When compared on a site-by-site basis, avian density at tamarisk sites was significantly greater than that at mesquite sites (two-sided Wilcoxon signed rank test, $P=0.032$ in 1984, $P=0.024$ in 1985).

There was no significant difference in the absolute number of species found on a site-by-site basis at mesquite and tamarisk sites in either 1984 or 1985 (two-sided Wilcoxon signed rank test, $P=0.67$ in 1984, $P=0.81$ in 1985). Likewise, no significant difference existed between the diversity indices (See Table 6) of

Table 2. Breeding bird densities (pairs/40 ha) at mesquite-dominated old-high-water-zone (OHWZ) study sites along the Colorado River in Grand Canyon, 1984.

	Pairs/40 ha at OHWZ Study Sites, 1984									
Species	1	2	3	4	5	6	7	8	9	10
Mourning Dove	0	25	26.7	0	66.7	0	0	0	29.4	88.8
Black-chinned Hummingbird	47	150	106.6	0	0	36.4	94	85.6	78.1	44.4
Costa's Hummingbird	23.5	0	26.7	100	0	0	0	0	29.4	0
Ash-throated Flycatcher	23.5	25	26.7	0	66.7	0	23.5	57.2	7.1	44.4
Bewick's Wren	47	50	53.4	0	0	0	0	85.6	7.1	0
Blue-gray Gnatcatcher	0	75	80.1	0	0	36.4	94	114.4	42.6	44.4
Phainopepla	0	0	0	0	0	0	0	0	14.2	0
Bell's Vireo	0	0	0	0	0	0	83.3	200.2	49.7	44.4
Lucy's Warbler	0	75	160.2	100	66.7	91	141	228.8	49.7	44.4
Yellow Warbler	0	0	26.7	0	0	0	11.7	14.3	0	0
Yellow-breasted Chat	23.5	13	0	0	0	0	23.5	57.2	7.1	0
Summer Tanager	0	25	26.7	0	0	0	23.5	0	0	0
Black-headed Grosbeak	12.5	0	0	0	0	0	0	0	0	0
Blue Grosbeak	23.5	0	26.7	0	0	0	23.5	0	7.1	0
Lazuli Bunting	0	25	0	0	0	0	0	0	0	0
Indigo Bunting	0	25	0	0	0	0	0	0	0	0
Brown-headed Cowbird	70.5	25	26.7	0	0	0	0	57.2	7.1	0
Hooded Oriole	0	0	0	0	0	0	0	28.6	0	0
House Finch	47	25	106.6	0	0	18.2	47	57.2	21.3	44.4
Lesser Goldfinch	0	0	53.4	0	0	0	0	0	7.1	44.4
No. of Species/Site	9	12	13	2	3	4	10	11	14	8
No. of Pairs/40 ha	318	538	747	200	200	182	565	986	357	400

Table 3. Breeding bird densities (pairs/40 ha) at mesquite-dominated old-high-water-zone (OHWZ) study sites along the Colorado River in Grand Canyon, 1985.

	Pairs/40 ha at OHWZ Study Sites, 1985									
Species	1	2	3	4	5	6	7	8	9	10
Mourning Dove	23.5	25	53.4	100	0	0	0	85.8	21.5	44.4
Black-chinned Hummingbird	23.5	25	80.1	0	66.7	18.2	47	57.2	21.5	133.2
Ash-throated Flycatcher	23.5	25	26.7	0	0	18.2	23.5	28.6	7.1	0
Bewick's Wren	0	50	53.4	0	0	0	0	57.2	7.1	0
Blue-gray Gnatcatcher	23.5	75	106.8	100	66.7	0	117.5	28.6	28.6	44.4
Phainopepla	0	0	0	0	0	0	0	0	7.1	0
Northern Mockingbird	0	0	0	0	0	0	0	0	14.2	44.4
Crissal Thrasher	0	0	0	0	0	0	0	28.6	0	0
Bell's Vireo	0	0	26.7	0	0	0	117.5	143	43.6	44.4
Lucy's Warbler	0	75	132.5	100	66.7	36.4	94	114.2	28.6	88.8
Yellow Warbler	0	0	0	0	0	0	23.5	28.6	0	0
Yellow-breasted Chat	11.8	0	0	0	0	0	70.5	85.8	14.2	0
Summer Tanager	0	0	0	0	0	0	0	14.2	0	0
Black-headed Grosbeak	11.8	0	0	0	0	0	0	0	0	0
Blue Grosbeak	11.8	0	0	0	0	0	0	14.2	7.1	0
Lazuli Bunting	0	25	0	0	0	0	0	28.6	0	0
Brown-headed Cowbird	70.5	0	26.7	0	0	0	0	28.6	14.2	0
Hooded Oriole	0	0	0	0	0	0	11.8	28.6	0	0
House Finch	0	0	53.4	0	0	0	0	114.2	7.1	0
Lesser Goldfinch	0	0	53.4	0	0	0	23.5	57.2	7.1	0
No. of Species/Site	8	7	10	3	3	3	9	17	14	6
No. of Pairs/40 ha	200	300	613	300	200	73	529	943	229	400

Table 4. Breeding bird densities (pairs/40 ha) at tamarisk-dominated new-high-water-zone (NHWZ) study sites along the Colorado River in Grand Canyon, 1984.

	Pairs/40 ha at NHWZ Study Sites, 1984									
Species	1	2	3	4	5	6	7	8	9	10
Mourning Dove	13.8	14.3	0	0	0	0	0	0	0	0
Black-chinned Hummingbird	13.8	42.9	117.5	0	100	100	114.2	80	40	0
Costa's Hummingbird	0	0	0	100	0	0	0	0	0	0
Willow Flycatcher	0	28.6	23.5	0	0	0	0	0	0	0
Ash-throated Flycatcher	0	28.6	23.5	0	0	0	0	0	0	0
Bewick's Wren	55.2	42.9	70.5	0	0	0	0	80	0	0
Marsh Wren	13.8	0	0	0	0	0	0	0	0	0
Blue-gray Gnatcatcher	41.2	57.2	70.5	0	100	300	114.2	160	40	0
Bell's Vireo	0	0	47	0	0	0	114.2	160	80	0
Lucy's Warbler	41.2	85.8	117.5	0	200	100	171.3	160	40	200
Yellow Warbler	27.6	28.6	70.5	0	0	100	114.2	240	0	0
Common Yellowthroat	13.8	14.3	23.5	400	0	0	114.2	80	40	0
Yellow-breasted Chat	69	42.9	47	0	0	0	57.1	80	0	0
Summer Tanager	0	14.3	23.5	0	0	0	0	0	0	0
Indigo Bunting	0	14.3	0	0	0	0	0	0	0	0
Great-tailed Grackle	13.8	0	0	0	0	0	0	0	40	0
Brown-headed Cowbird	55.2	28.6	94	0	0	0	57.1	0	200	0
Hooded Oriole	0	0	23.5	0	0	0	0	80	0	0
Northern Oriole	13.8	0	0	0	0	0	0	0	0	0
House Finch	55.2	28.6	165.5	0	0	0	0	0	0	0
Lesser Goldfinch	13.8	14.3	23.5	0	0	0	0	80	0	0
No. of Species/Site	14	15	15	2	3	4	8	10	7	1
Total No. Pairs/40 ha	441	486	941	500	400	600	857	1200	480	200

Table 5. Breeding bird densities (pairs/40 ha) at tamarisk-dominated new-high-water-zone (NHWZ) study sites along the Colorado River, 1985.

	Pairs/40 ha at NHWZ Study Sites, 1985									
Species	1	2	3	4	5	6	7	8	9	10
American Coot	13.8	0	0	0	0	0	0	0	0	0
Western Screech-Owl	0	0	23.5	0	0	0	0	0	0	0
Mourning Dove	41.4	28.6	23.5	0	100	0	57.1	0	0	200
Black-chinned Hummingbird	0	113.4	165.5	100	100	200	114.2	160	80	0
Willow Flycatcher	0	28.6	23.5	0	0	0	0	0	0	0
Ash-throated Flycatcher	13.8	28.6	23.5	0	0	0	0	0	0	0
Bewick's Wren	69	42.9	70.5	0	0	0	0	80	0	0
Blue-gray Gnatcatcher	27.6	71.5	70.5	0	0	50	57.1	80	0	0
Bell's Vireo	0	0	0	0	0	0	114.2	160	0	200
Lucy's Warbler	82.8	85.8	117.5	0	100	50	171.3	80	0	0
Yellow Warbler	0	28.6	47	0	100	0	171.3	160	0	0
Common Yellowthroat	27.6	14.3	23.5	0	0	0	57.1	80	40	0
Yellow-breasted Chat	55.2	57.2	23.5	0	0	0	171.3	80	0	0
Summer Tanager	0	0	0	0	0	0	57.1	40	0	0
Blue Grosbeak	0	14.3	0	0	0	0	0	40	0	0
Lazuli Bunting	0	14.3	0	0	0	0	57.1	0	0	0
Great-tailed Grackle	27.6	0	23.5	0	0	0	0	80	40	0
Brown-headed Cowbird	27.6	42.9	47	0	0	0	0	0	0	0
Hooded Oriole	0	0	23.5	0	0	0	0	0	0	0
Northern Oriole	13.8	0	0	0	0	0	0	0	0	0
House Finch	138	0	94	0	0	0	0	80	0	0
Lesser Goldfinch	0	0	23.5	0	0	0	57.1	80	60	0
House Sparrow	13.8	0	0	0	0	0	0	0	0	0
No. of Species/Site	13	13	16	1	4	3	11	13	4	2
Total No. airs/40 ha	552	571	824	100	400	300	1085	1200	220	400

mesquite sites as compared to tamarisk sites (two-sided Wilcoxon signed rank test, P=0.55 in 1984, P=1.0 in 1985).

Percent woody vegetation cover in tamarisk (See Table 7) was slightly higher than that in mesquite (See Table 8), but the difference was not significant (two-sided Wilcoxon signed rank test, P=0.36). Mean canopy height in tamarisk exceeded that of mesquite (See Table 9), but the difference was not significant (two-sided Wilcoxon signed rank test, P=0.08).

Species composition differed between mesquite and tamarisk sites. Three species occurred largely, but not exclusively, in mesquite: Phainopepla (*Phainopepla nitens*), Northern Mockingbird (*Mimus polyglottos*), and Black-headed Grosbeak (*Pheucticus melanocephalus*) (Tables 2 and 3). Phainopeplas and Northern Mockingbirds were occasionally observed in tamarisk at times other than census periods. The Black-headed Grosbeaks, which were recorded only at mesquite site 01-A, ranged widely over both habitat types, and their nest was located in tamarisk adjacent to the study site.

Ten species occurred largely or exclusively in tamarisk habitats (See Tables 4 and 5). At least 90% of the overall populations of these species occurred in tamarisk. These included: Willow Flycatcher (*Empidonax trailii*), Yellow Warbler, Common Yellowthroat, Yellow-breasted Chat (*Icteria virens*), Northern Oriole (*Icterus galbula*), Great-tailed Grackle (*Quiscalus mexicanus*), American Coot (*Fulica americana*), Marsh Wren (*Cistothorus palustris*), Western Screech-Owl (*Otus kennicottii*), and House Sparrow (*Passer domesticus*) (See Tables 4 and 5). Most of the species which occurred largely or exclusively in tamarisk were obligate riparian birds (Johnson et al., 1977). Obligate species were those restricted entirely to well-developed riparian vegetation in the southwestern United States.

More species occurred exclusively in tamarisk habitats, although no significant difference existed between the total number of species or diversity indices of tamarisk compared to mesquite on a site-by-site basis. Ten species (35%) occurred largely or exclusively in tamarisk, compared to only three species (10%) which occurred largely in mesquite. Of the 29 total species recorded in the two habitat zones, 16 (55%) occurred throughout both habitats (See Tables 2-5): Mourning Dove, Black-chinned and Costa's Hummingbirds, Ash-throated Flycatcher, Bewick's Wren (*Thryomanes bewickii*), Blue-gray Gnatcatcher, Bell's Vireo (*Vireo bellii*), Lucy's Warbler, Summer Tanager (*Piranga rubra*), Blue Grosbeak (*Guiraca caerulea*), Lazuli and Indigo Buntings (*Passerina amoena* and *P. cyanea*), Brown-headed Cowbird, Hooded Oriole (*Icterus cucullatus*), House Finch, and Lesser Goldfinch (*Carduelis psaltria*).

Discussion

The finding of this study that breeding bird density was significantly greater in tamarisk as compared to mesquite

Table 6. Diversity indices (H') for breeding birds at mesquite-dominated and tamarisk-dominated study sites along the Colorado River in Grand Canyon, 1984-85. Site numbers correspond to those used in Table 1.

Study Areas	1984 H' Values		1985 H' Values	
	Mesquite	Tamarisk	Mesquite	Tamarisk
01	.9017	1.0620	.8141	.9517
02	.9611	1.1085	.7904	1.0237
03	1.0143	1.1761	.5908	1.0902
04	.3010	.3010	.4771	0
05	.4771	.4771	.4771	.6021
06	.5300	.5396	.4515	.3768
07	.9940	.8800	.8141	.9894
08	.9294	.6065	1.0605	1.0757
09	1.0029	.7378	1.0628	.5829
10	.8874	0	.7283	0

Table 7. Percent vegetative cover by species for tamarisk-dominated study sites along the Colorado River. Site numbers correspond to those used in Table 1.

	Tamarisk Study Sites									
Species	1	2	3	4	5	6	7	8	9	10
Baccharis spp.	0	11	0	0	5	15	6	6	4	0
Phragmites australis	0	0	0	0	0	0	17	0	0	0
Salix gooddingii	3	0	34	0	0	0	0	0	0	0
Tamarix chinensis	63	71	60	50	30	23	50	54	37	18
Tessaria sericea	4	0	0	0	0	0	15	19	28	17
Other Woody Species	0	6	0	0	5	0	6	5	0	0
Total Cover (%)	70	88	94	50	40	38	94	84	69	35

Table 8. Percent vegetative cover by species for mesquite-dominated study sites along the Colorado River. Site numbers correspond to those used in Table 1.

	Mesquite Study Sites									
Species	1	2	3	4	5	6	7	8	9	10
Acacia greggii	0	0	1	5	18	45	19	1	9	9
Celtis reticulata	7	0	0	0	0	0	0	14	0	0
Fraxinus anomala	14	0	0	0	0	0	0	0	0	0
Prosopis glandulosa	0	73	56	0	0	2	37	70	50	27
Quercus turbinella	22	0	0	0	0	0	0	0	0	0
Other woody species	9	7	14	26	32	13	23	4	13	22
Total Cover (%)	52	80	71	31	50	60	79	89	72	58

Table 9. Maximum canopy height in mesquite and tamarisk study sites along the Colorado River. Site numbers correspond to sites described in Table 1.

	Maximum Canopy Height (m)			
	Mesquite		Tamarisk	
Site Number	Mean	Range	Mean	Range
01	1.0	0-4.5	3.8	0-7.0
02	1.6	0-5.5	3.7	0-7.0
03	1.5	0-5.5	4.7	0-12.0
04	0.3	0-1.0	0.9	0-4.0
05	0.7	0-2.5	0.8	0-2.0
06	1.8	0-4.0	0.9	0-4.0
07	1.5	0-3.5	2.3	0-5.5
08	3.0	0-5.5	3.0	0-6.0
09	1.9	0-4.5	1.4	0-4.5
10	1.5	0-4.0	2.1	0-3.0
Overall Mean and Range	1.5	0-5.5	2.4	0-12.0

habitats was in contrast to most previous studies. Anderson et al. (1977) reported that both pure tamarisk and mixed-tamarisk habitats supported fewer birds/40 ha than native mesquite habitats on the Lower Colorado River, as did Cohan et al. (1978). Hunter et al. (1985) reported that a greater proportion of bird populations preferred mesquite over tamarisk habitats in a much larger study area along the Lower Colorado River and Rio Grande. The Pecos River, however, was the only geographic area where avian density patterns in mesquite and tamarisk were similar to this study. There, 75% of bird populations examined showed a preference for tamarisk over mesquite habitats (Hunter et al., 1985).

Willson (1974) and Stamp (1978) reported that bird species diversity was linearly correlated with foliage height diversity. Bird species diversity was also curvilinearly correlated with percent vegetative cover (Willson, 1974). Maximum vegetative height and percent vegetative cover between tamarisk and mesquite habitats in this study was not significantly different. This relationship was partially responsible for the similarity in overall bird species diversity and absolute number of bird species breeding in tamarisk and mesquite habitats. However, Anderson et al. (1977) and Cohan et al. (1978) reported native mesquite habitats exhibited a greater number of bird species than tamarisk habitats of similar structure.

Mean avian densities in mesquite habitats sampled from 1984-85 were comparable to or slightly less than the 476 pairs/40 ha reported from mesquite in southern Arizona (Gavin and Sowls, 1975), but generally exceeded avian densities reported from mesquite in other areas of the Southwest. Austin (1970) reported 45-49 pairs/40 ha from mesquite in southern Nevada, Anderson et al. (1977) and Cohan et al. (1978) documented 131-150 pairs/40 ha in mesquite along the Lower Colorado River, and Stamp (1978) identified 244 pairs/40 ha in mesquite from central Arizona.

Avian densities of individual, poorly-developed mesquite sites in this study (4-A, 5-A, 6-A) were equivalent to most density values reported from the Southwest. However, the 747 to 613 pairs/40 ha documented at Cardenas Creek (site 3-A) and the 986 to 943 pairs/40 ha from Parashant Wash (8-A) were exceptionally high. These well-developed mesquite sites exhibited the highest avian densities ever reported from that community.

Avian density at tamarisk sites reported from southern Arizona have varied from approximately 100 to 388 pairs/40 ha (Anderson et al., 1977; Cohan et al., 1978; Szaro and Jakle, 1982). Avian densities at individual, poorly-developed tamarisk sites examined in this study (4-B, 5-B, 6-B, 10-B) were comparable to those reported densities, but mean avian density in tamarisk greatly exceeded reported densities. Certain well-developed tamarisk sites (3-B, 7-B, 8-B) exhibited avian densities in excess of 800

pairs/40 ha, making them comparable with the highest densities ever reported for non-colonial breeding birds in North America (Carothers et al., 1974; Willet and Van Velzen, 1984).

Intensive nest searches after each census period provided a complementary check on the degree of accuracy of the census data. For example, census data from the tamarisk-dominated site at Cardenas Marsh (3-B) indicated 35 pairs of birds in the 1.7 ha area, for a comparative density of 824 pairs/40 ha (See Table 5). A nest search through approximately half of the site after the June census revealed 18 active nests. In comparative figures, the 18 active nests in only half the study area accounted for 410 (50%) of the 824 pairs/40 ha indicated by census data. This accountability rate suggested high accuracy of census data.

Several factors may have contributed to high avian density at tamarisk (and some mesquite) sites. The small, linear study sites exhibited very high edge: area ratios compared to other studies of avian density in riparian areas (Carothers et al., 1974; Gavin and Sowls, 1975; Anderson et al., 1977; Cohan et al., 1978; Stamp, 1978; Szaro and Jakle, 1982). A high edge: area ratio would have accentuated the edge effect (Odum, 1959; Johnson, 1978) toward increased population densities at community junctions.

Social organization of riparian bird communities may have also contributed to high avian densities. Carothers et al. (1974) reported that on riparian areas of high avian density, the frequency of class-A territories may decline to allow birds to forage freely outside of the riparian habitat. By calculating comparative avian densities (pairs/40 ha) based only on the extent of riparian habitat involved, a much higher avian density was obtained. This was the case for Black-chinned Hummingbirds in this study, whose abundant nests were concentrated in tamarisk. Foraging flights, however, often took hummingbirds long distances from riparian areas to forage in both desertscrub and over the river itself.

Abundance of food resources could have contributed to high avian densities, especially in tamarisk habitats. Tamarisk habitats have developed since 1963 and were in an early successional stage of vegetative development. Net community production and biomass accumulation were found to be higher in early successional stages (Odum, 1969). These conditions could have accounted for the extremely high insect densities that were found in tamarisk habitats in the study area (Stevens, 1976). High insect densities would have facilitated smaller avian territory size and hence higher avian density per unit area.

The input of aquatic insects emerging from the river into the adjacent riparian zones could have also contributed to an abundance of food resources for breeding birds. This input was

reported to be substantial in the study area (Stevens, 1976). Territory size has been shown to decrease with increasing food resources (Gill and Wolf, 1975).

Hunter et al. (1985) originally suggested the need for regional strategies toward the management of tamarisk as avian habitat, based on contrasting findings from three southwestern river systems. The findings of this study supported that contention. Species composition and avian density in tamarisk along the Grand Canyon section of the Colorado River were sufficiently different from that reported from other geographic areas to warrant a unique regional approach to tamarisk management. Findings from the Lower Colorado River indicated that most birds do not use tamarisk in high proportions compared with native plant communities (Hunter et al., 1985), and that avian density in tamarisk was low (Anderson et al., 1977). Use of these geographically distant findings to direct tamarisk management for breeding birds in Grand Canyon would clearly be inappropriate.

CHAPTER 3

NESTING HABITAT RELATIONSHIPS OF RIPARIAN BIRDS

Introduction

The niche-gestalt of James (1971) established that a predictable relationship existed between birds and their required breeding habitat. The niche-gestalt, as a basic physical form of the ecological niche, has been established as a working model with the ability to distinguish between species in studies on avian nesting habitat and nest site selection (Smith, 1977; Conner and Adkisson, 1977; Raphael, 1981; MacKenzie and Sealy, 1981; MacKenzie et al., 1982). However, avian habitat ordination has been examined primarily in widespread upland vegetation types as opposed to riparian vegetation.

Little is known of avian habitat ordination and nest site selection in riparian scrubland communities of the southwestern United States dominated by tamarisk (Whitmore, 1975, 1977; Rice et al., 1983). Tamarisk is a widespread, exotic shrub of low-elevation riparian areas in the Southwest and dominates over 100,000 ha of streamside habitat in Arizona, California, New Mexico, and west Texas (Horton, 1977). Avian community organization in tamarisk differs from that of native riparian habitats (Hunter et al., 1985), a contrast which calls for habitat-specific management strategies. A more thorough understanding of avian habitat selection in tamarisk would aid in management of southwestern riparian birds.

This study describes nesting habitat relationships of riparian birds in 20-year-old tamarisk scrubland along the Colorado River in Grand Canyon National Park. The objective was to determine the extent of difference between species with respect to nesting habitat selection by a community of riparian birds in order to characterize breeding habitat by species. Obligate riparian birds were chosen for study since they are completely dependent on riparian habitat for breeding in a particular geographic area (Johnson et al., 1977). This habitat dependence is most obvious in the desert lowlands of the Southwest, where water is the main limiting factor and where productivity and structure of riparian vegetation is markedly dissimilar from that of the adjacent upland.

Study Area

The study area was the 389 km riparian corridor of the Colorado River from Glen Canyon Dam (elevation 955 m) downstream to the mouth of Diamond Creek (elevation 410 m). This riparian corridor

lies entirely within the boundaries of Glen Canyon National Recreation Area and Grand Canyon National Park, Arizona.

The completion of Glen Canyon Dam in 1963 marked an end to annual floods which had scoured away all woody vegetation below the predam high water line along this section of the Colorado River. A dense new riparian scrubland, the new-high-water-zone, developed in the predam scour zone in the absence of flooding (Turner and Karpiscak, 1980). This tamarisk-dominated habitat also included dense, largely monotypic stands of tamarisk, coyote willow arrowweed, and seepwillow.

Prior to construction of the dam, woody riparian vegetation in the river corridor had been limited to honey mesquite and catclaw acacia in the old-high-water-zone, located adjacent to and just above the predam scour zone. This mesquite-dominated vegetative zone persisted as a relict habitat after construction of the dam, so that both habitat zones were present during the study period as adjacent, parallel strands running discontinuously along the riverbank.

Methods

Nests were located at a number of sites in the river corridor by systematic ground searches of both riparian zones. Primary sites were Lees Ferry, Saddle Canyon, Cardenas Marsh, Stairway Canyon, Lava Falls, Whitmore Wash, Parashant Wash, and Granite Park. Up to six skilled observers assisted in searches from April through July, 1982-85. Behavior of adult birds revealed the location of many nests. Time spent searching each riparian habitat zone was in direct proportion to the extent of each habitat at individual study sites. For example, the mesquite: tamarisk ratio of nest searching time was 25:75 at sites whose vegetation consisted of one-fourth honey mesquite in the old-high-water-zone and three-fourths tamarisk in the new-high-water-zone.

Active nests as well as those that were vacated within the present or previous breeding season but were still identifiable were used in the analyses. Positive identification of vacated nests could be made only for Bell's Vireo, Common Yellowthroat, and Hooded and Northern (Bullock's) orioles.

Nest sites were used as points around which to measure 13 habitat variables (Collins, 1981). Variables were measured in 0.04 ha circular plots centered at nest sites (James and Shugart, 1970; James, 1971).

The height of the tallest vegetation within each circular plot was measured to the nearest 1 m. Total number of trees (i.e., woody vegetation >7.5 cm diameter-breast-high (dbh) within each plot was counted. Length of edge (Martinka, 1972) was measured

in each circular plot. Edge was the border between a patch of vegetation and an open area (Martinka, 1972), or between patches of different structure.

Shrub counts of the six most abundant species or groups of species in the river corridor were recorded in two perpendicular armlength transects (north-south, east-west) at dbh across the center of each circular plot. These species or groups of species included honey mesquite, tamarisk, coyote willow, the seepwillow and waterweed complex (*Baccharis sarothroides* and *B. sergiloides*), the *Baccharis emoryi* and *B. salicifolia* complex, and arrowweed. The four species of *Baccharis* were treated as two complexes due to their ecological, structural, and taxonomic similarity (Turner and Karpiscak, 1980). Shrubs included woody vegetation at least 1.5 m in height with a dbh of less than 7.5 cm.

An index to percent foliage volume was calculated using frequency counts of foliage in four foliage layers (0-1 m, 1-2 m, 2-3 m, >3 m) in each circular plot (Mauer and Whitmore, 1981). Frequency counts were made at 20 non-biased points in each plot, where five points were equidistant along each of four (north, south, east, west) lines radiating out from the plot center. At each point, presence or absence of foliage (living or dead plant material) in each layer was recorded. The resulting frequency represented the probability of encountering foliage in any layer within a given distance around nests.

Discriminant analysis (DA) was used to classify species based on habitat variables. Standard transformations were performed on the raw data to comply with the normality assumption. The DA created a habitat representation space based on data for the five most common species of birds (Bell's Vireo, Yellow Warbler, Common Yellowthroat, Yellow-breasted Chat, and Northern [Bullock's] Oriole). The final DA employed only the ten habitat variables that contributed substantially to species classification. Therefore, the following variables were excluded: foliage volume from 0-1 m, the shrub count of mesquite, and the shrub count of the *Baccharis emoryi* and *salicifolia* complex. Nest sites were classified using individual covariance matrices for each species (Gnanadesikan, 1977). Computations were performed using Statistical Package for the Social Sciences software (Nie et al., 1975).

The representation space constructed by the DA for the five common species was used to analyze all eleven bird species. Positions within the habitat representation space of each of six species with small sample sizes (<10 nests) were manually plotted using values calculated by the DA. Average habitat preferences were analyzed by comparing species means. Habitat dispersion was analyzed by computing species covariance matrices and considering (1) species standard deviation in the first discriminant

coordinate and (2) species concentration ellipsoid in the first two discriminant coordinates. Concentration ellipsoids were calculated at one standard deviation from the species mean habitat preferences. A pairwise measure of statistical distance between species was derived in three dimensions. The statistic used was the square root of the test statistic proposed by James (1954) for use in a two-sample problem with multivariate normal distributions having unequal covariance matrices.

Results and Discussion

Eleven species of obligate riparian breeding birds were recorded (See Table 10). These species may occur in mesic nonriparian situations in other parts of their range in North America, and are solely dependent upon riparian habitats only in the desert Southwest (Johnson et al., 1977). Bell's Vireos occasionally breed in dense, nonriparian vegetation of the Southwest lowlands. In the Grand Canyon region, however, the dense lowland vegetation Bell's Vireo requires occurred only in riparian areas. In the Southwest, American Coot and Common Yellowthroat are more commonly associated with marshy habitats, while Great-tailed Grackle is normally limited to agricultural and urban areas (artificial riparian) (Johnson et al., 1977). The class of obligate riparian birds recognized here encompassed these three species.

A preliminary DA correctly classified the habitat zone (mesquite or tamarisk) for 94% of the nest sites. Variables most important in distinguishing between species were numbers of honey mesquite and tamarisk shrubs and the amount of foliage volume above 3 m. The final DA was restricted to tamarisk habitats, where 90% of the nests occurred. The sample size of nests located in mesquite habitats was too small to merit its inclusion in the final analysis, as Bell's Vireo was the only species nesting widely in mesquite (See Table 10).

Analysis of the five most common species using ten habitat variables correctly classified 64% of all nests located in tamarisk habitats (Table 11). All Common Yellowthroat nests were correctly classified and nearly perfect classification was achieved for Northern (Bullock's) Oriole. Bell's Vireo nests were correctly classified in more than half the cases. However, Yellow Warbler nests were incorrectly classified in more than half of all cases, and even poorer classification was obtained for Yellow-breasted Chats. DA was unable to differentiate well between warblers and chats because of an overlap in their nesting habitat.

Three discriminant functions explained 96% of the variation between these five species (See Table 12). This was a higher

Table 10. Species of obligate riparian birds along the Colorado River in Grand Canyon National Park, 1982-85.

Species	Species Code	Status[1]	Total Sample (N)	No. of Nests OHWZ[2]	No. of Nests NHWZ[3]	% in NHWZ
American Coot	AC	R,r	3	0	3	100
Willow Flycatcher	WF	R,r	8	0	8	100
Bell's Vireo	BV	C,w	47	9	38	81
Yellow Warbler	YW	C,w	20	1	19	95
Common Yellowthroat	CY	C,w	15	0	15	100
Yellow-breasted Chat	YbC	C,w	21	2	19	90
Blue Grosbeak	BG	U,w	4	1	3	75
Indigo Bunting	IB	R,w	2	1	1	50
Great-tailed Grackle	GtG	U,w?	1	0	1	100
Hooded Oriole	HO	U,r	7	0	7	100
Bullock's Oriole	BO	C,r	11	0	11	100
Total			139	14	125	$\bar{X}$=90

[1]Abundance codes: C = abundant to common, U = fairly common to uncommon, R = rare. Distribution codes: w = widespread where riparian vegetation is present, r = geographically restricted. ? = Uncertain or in a state of change.

[2]OHWZ = old-high-water-zone

[3]NHWZ = new-high-water-zone

Table 11. Classification of the five common species of riparian birds analyzed in the Discriminant Analysis.

Actual Species	Number of Cases	Discriminant Analysis Results				
		Bell's Vireo	Yellow-breasted Chat	Yellow Warbler	Bullock's Oriole	Common Yellow-throat
Bell's Vireo	38	25	7	1	1	4
Yellow-breasted Chat	19	3	6	6	2	2
Yellow Warbler	19	1	3	9	3	3
Bullock`s Oriole	11	0	0	1	10	0
Common Yellowthroat	15	0	0	0	0	15

Overall percent of cases correctly classified = 63.7%.

percentage than that achieved by most previous habitat ordination models (James, 1971; Connor and Adkisson, 1977; Raphael, 1981).

The first discriminant function loaded primarily on the number of *Baccharis sarathroides* and B. *sergiloides* shrubs, maximum canopy height, number of tamarisk shrubs, and length of edge (See Table 12). The first function was therefore primarily associated with three interrelated factors: (1) the relative density of the most common and widespread shrub or shrub group (decreasing values indicate increasing shrub density), (2) overall vegetative height (increasing values indicate taller vegetation), and (3) habitat patchiness (increasing values indicate more patchy habitats). Length of edge was a rough, but effective index to habitat patchiness because edge indicated the relative amount of border between vegetation and open areas, an amount which would increase with increasing patchiness. The need for such an index was suggested by James (1978) although Martinka (1972) had previously found length of edge to be a significant factor in the habitat preferences of Blue Grouse (*Dendragapus obscurus*). The first function accounted for 53% of the variance.

The second function loaded primarily on three foliage volume variables (1-2 m, 2-3 m, >3 m) and number of trees present (Table 12). Increasing values on the second function were correlated with habitats containing more trees and more foliage volume from 2-3 m. Decreasing values indicated habitats exhibiting fewer trees and more foliage volume from 1-2 m. Decreasing values, therefore, were associated with marsh or scrub habitats of low height, while increasing values were associated with more typical habitats of greater height away from the water's edge. This function accounted for 31% of the variation.

The third function loaded primarily on foliage volume above 3 m, number of trees present, and maximum canopy height (See Table 12). The third function accounted for 12% of the variance.

Average habitat preferences of each species were indicated by plotting species mean vectors in three-dimensional habitat space (Figure 1). The first discriminant function separated species into three general classes (See Figure 1). The first class (smallest scores on the first function) preferred lower, denser vegetation dominated by tamarisk and *Baccharis* shrubs. This class included Bell's Vireo, Common Yellowthroat, and Yellow-breasted Chat, species associated with earlier successional stages of riparian vegetation. This association was similar to that found by Whitmore (1975, 1977) for yellowthroats and chats along the Virgin River of Utah. The second class (largest scores on first function) preferred a combination of vegetation that was either taller, patchier (more open), or exhibited fewer tamarisk and *Baccharis* shrubs. This class included the grackle, coot, and Northern (Bullock's) Oriole, species associated with restricted

Table 12. Standardized canonical discriminant function coefficients of habitat variables resulting from the discriminant analysis of riparian breeding bird habitat along the Colorado River.

Variable	Function 1	Function 2	Function 3
Percent of total variance accounted for	53.4	31.0	12.2
Cumulative percent of variance accounted for	53.4	84.4	96.6
Standardized coefficients			
Length of edge	.387	-.147	.327
Foliage volume, 1-2 m	-.072	-.991	.351
Foliage volume, 2-3 m	.380	1.265	.161
Foliage volume, >3 m	-.184	-.454	-.978
Tallest plant in plot	.419	-.061	.403
Total no. of trees	.293	.543	.912
No. tamarisk shrubs	-.394	-.058	.254
No. *Baccharis* shrubs	-.587	.248	.259
No. coyote willow shrubs	.259	.142	-.017
No. arrowweed shrubs	-.230	.040	-.041

habitat types in the study area (See Table 10). Whitmore (1975, 1977) also associated Northern (Bullock's) Oriole with taller vegetation composed of larger trees. The third class was composed of species whose habitat preferences were intermediate to the above, including Willow Flycatcher, Yellow Warbler, Blue Grosbeak, Hooded Oriole, and Indigo Bunting.

The second discriminant function was useful in separating marsh-nesting species from those that preferred more trees or more foliage volume above 2 m (See Figure 1). Common Yellowthroat, coot, and grackle preferred marshy habitats with dense foliage up to approximately 2 m.

The third discriminant function did not separate any major class of species (See Figure 1). Instead, the third function refined the discrimination based on complex interactions between original habitat variables. This function loaded strongly on total number of trees and foliage volume above 3 m, but in opposite directions. Further differentiation was achieved for Hooded and Northern (Bullock's) orioles, Willow Flycatcher, and Yellow Warbler with this function. These four species were only slightly dissimilar in their preference for taller vegetation. However, the third function indicated that it was the structure of taller vegetation that separated species. The flycatcher and warbler preferred tall vegetation with more foliage volume above 3 m and fewer trees, while orioles preferred tall vegetation with less foliage volume above 3 m and more trees.

An index to the range of habitat use for each species was obtained by comparison of the species standard deviation with respect to the first discriminant function (See Table 13). A complementary analysis compared species concentration ellipsoids in the first two discriminant functions (See Figure 2).

The species with the largest range of habitat use (generalist) was Bell's Vireo (See Figure 2). American Coot exhibited the smallest range of habitat use (specialist) (See Table 13), although Figure 2 reveals that it had a slightly wider range of overall habitat use than Blue Grosbeak. Bell's Vireo and Willow Flycatcher were the most extreme habitat generalists in the river corridor, while Yellow Warbler, Yellow-breasted Chat and Hooded Oriole were moderate generalists. Common Yellowthroat and Northern (Bullock's) Oriole were moderate specialists. The most extreme specialization was shown by the grosbeak and coot.

Locations of species mean vectors illustrated approximate similarity of habitat use between species. Figure 1 did not, however, take into account differences in range of habitat use that were observed. Simultaneous plotting of species concentration ellipsoids (Figure 2) illustrated the effective overlaps in habitat use. American Coot was the only species whose ellipsoid did not overlap with any other species (Figure 2). The

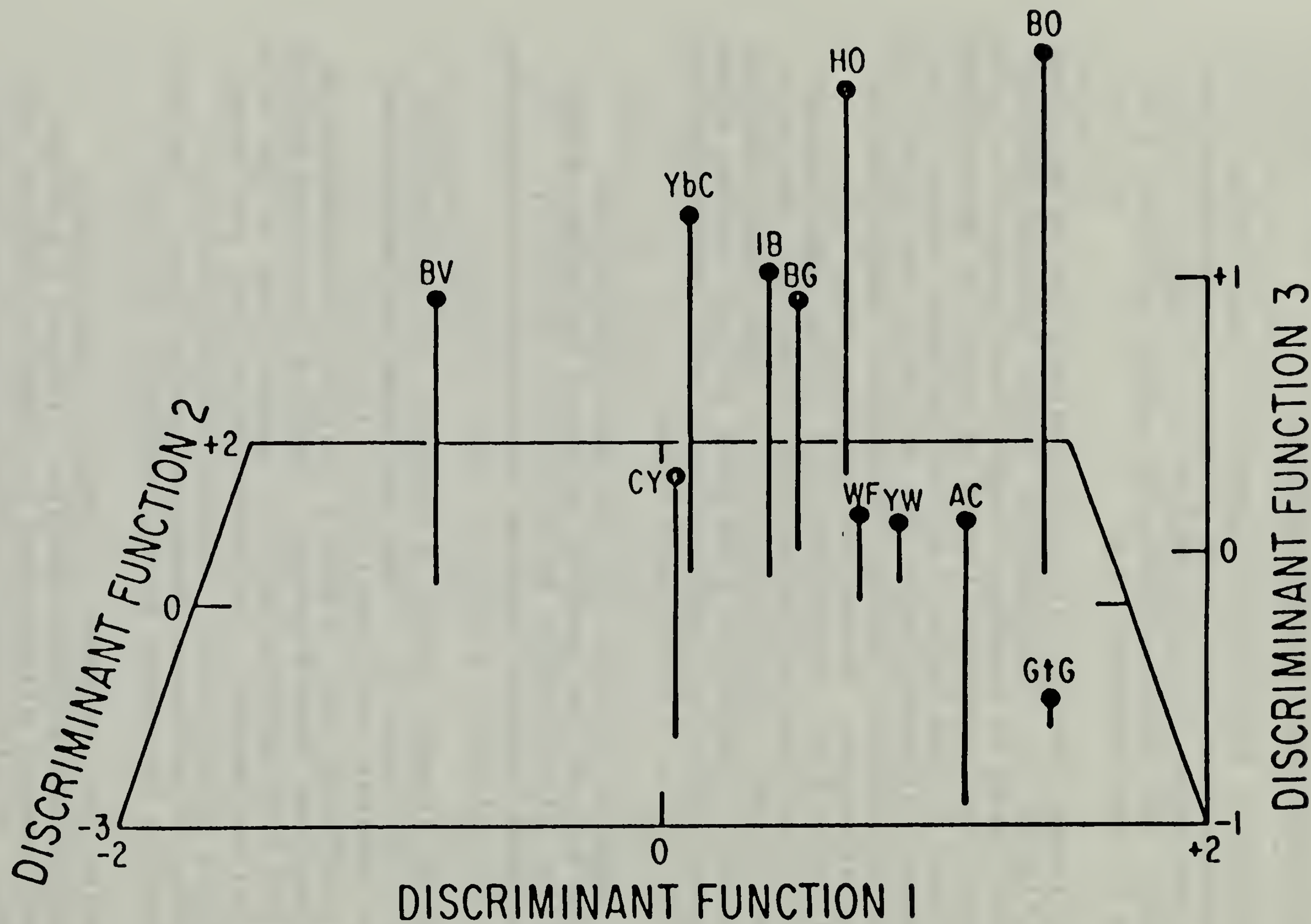

Figure 1. Average habitat preferences of riparian birds along the Colorado River in Grand Canyon National Park, Arizona, in three-dimensional space, as indicated by species mean vectors. Species codes as in Table 10.

Table 13. Nesting habitat generalist and specialist species of riparian birds within the new-high-water-zone of the Colorado River as indicated by values of standard deviation in the first discriminant function of each species. Only those birds with sample sizes larger than one are indicated.

Standard deviation of discriminant function 1	Species	Range of habitat use
1.22	Bell's Vireo	Relative Habitat Generalist
1.15	Willow Flycatcher	
.98	Yellow Warbler	
.97	Yellow-breasted Chat	
.97	Hooded Oriole	
.62	Common Yellowthroat	
.44	Bullock's Oriole	
.19	Blue Grosbeak	
.17	American Coot	Specialist

Common Yellowthroat ellipsoid only overlapped that of Willow Flycatcher. The flycatcher's ellipsoid was the largest, totally encompassing those of Yellow Warbler, Blue Grosbeak, and Northern (Bullock's) Oriole, and partially encompassing those of the vireo, chat, and Hooded Oriole.

These similarities were quantified by computation of statistical distances between species means (Table 14). Small distances represented similarity in habitat use between species pairs; large distances indicated dissimilarity. American Coot and Bell's Vireo were the most dissimilar species in their use of habitat. Moreover, American Coot and Bell's Vireo were consistently most different from other species. Willow Flycatcher and Yellow Warbler were the two species consistently most similar to all other species in their breeding habitat choice. Willow Flycatcher and Yellow Warbler were also the two most similar species, a relationship which was reinforced by the observation that active nests of the two species were occasionally found less than 4 m apart. The flycatcher and

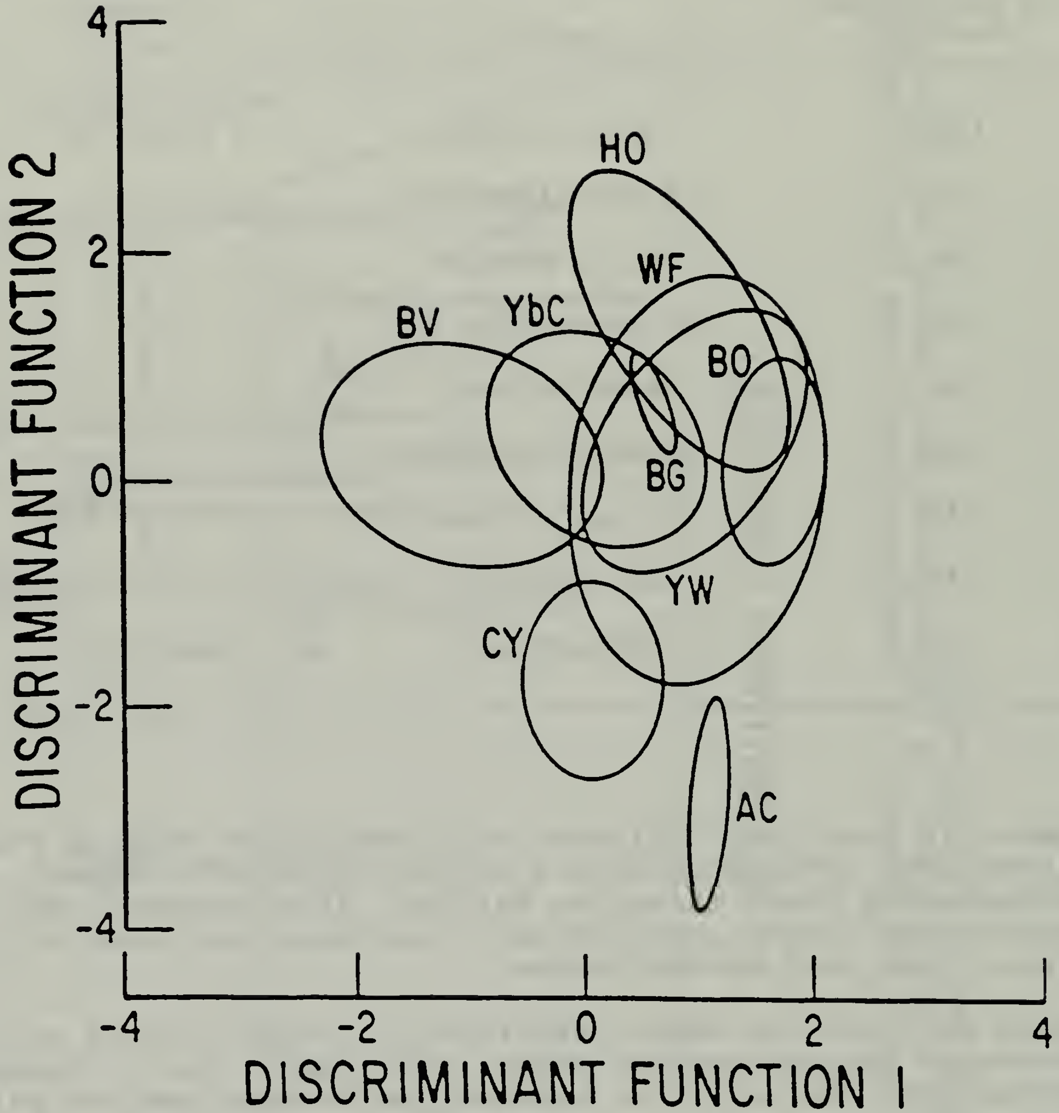

Figure 2. Simultaneous plot of species concentration ellipsoids in two-dimensional habitat space for each of the nine species of riparian birds along the Colorado River in Grand Canyon National Park, Arizona, with a sample size of at least three nests.

Species codes as in Table 10.

Table 14. Statistical distances between mean nesting habitat preferences of riparian birds along the Colorado River, based on all three functions. Only those species with a sample size of greater than or equal to three nests are included. Species codes as in Table 10.

	Relative statistical distances*							
Species	WF	BV	YW	CY	YbC	BG	HO	BO
American Coot	3.6	15.2	6.5	6.8	9.1	6.9	8.3	7.5
Willow Flycatcher		5.5	0.6	4.2	2.9	1.4	2.3	2.8
Bell's Vireo			7.1	8.1	4.2	10.1	9.2	11.7
Yellow Warbler				6.3	3.7	1.8	5.9	6.2
Common Yellowthroat					7.3	10.8	11.8	10.5
Yellow-breasted Chat						3.2	5.1	6.6
Blue Grosbeak							2.4	8.1
Hooded Oriole								3.4

* As indicated by the square root of the James test statistic.

warbler could be managed as one species in the study area. However, the danger of identifying groups of similar species has been pointed out by James (1971), who noted that variable choice may influence results to such an extent that caution is advised in interpretation of group relationships.

Another approach to habitat similarity was to consider the proximity of each species to the average nesting habitat exploited by all species. Thus, species ellipsoids which were farthest from the center of the habitat space represented the most atypical habitats (See Figure 2). American Coot and Northern (Bullock's) Oriole were farthest from the central habitat space.

From a management perspective, regularly-breeding species with the most unusual or restricted habitat are those which require special attention. For example, Northern (Bullock's) Oriole was a common, regularly-breeding species in the study area (See Table 10), was a moderate habitat specialist (See Table 13), and had a small concentration ellipsoid that was displaced from the central habitat space (See Figure 2). Therefore, Northern (Bullock's)

Oriole belonged in this management category, because if the status quo for its specialized habitat was not maintained, the species could be reduced in numbers and distribution. In contrast, American Coot only nested rarely and irregularly in the study area during seasons when water releases from Glen Canyon Dam were unusually high and stable. Even though American Coot was also a habitat specialist which had a small concentration ellipsoid, its irregular occurrence did not place it in the same management attention category as Northern (Bullock's) Oriole.

Caution should be exercised in making inferences about the six rarer species due to small sample sizes involved. The size of their concentration ellipsoids suggested that the data were reliable (note how tightly clustered were the nest sites of American Coot and Blue Grosbeak, each with a sample size of only three). Nevertheless, only a small amount of additional data could substantially change their average habitat preferences indicated in the DA. Moreover, since habitat space was constructed without reference to these six rarer species, variables may have been omitted that were critical. For example, the Willow Flycatcher, here identified as a generalist (See Table 13), with a restricted distribution (See Table 10), could possibly specialize with respect to a variable not included in the DA.

The tamarisk-dominated habitats were in a relatively early stage of vegetational succession. Avian species composition and average habitat preferences within the rapidly-developing tamarisk habitats can be expected to change with the passage of time and continued plant succession. Management should consider avian relationships with these changes in mind and allow for decision-making flexibility as succession proceeds.

CHAPTER 4

NEST PLACEMENT PREFERENCES OF RIPARIAN PASSERINES IN A TAMARISK COMMUNITY

Introduction

Tamarisk has been identified as poor nesting habitat, relative to native vegetation, for many riparian passerines along the lower Colorado River (Anderson et al., 1977; Cohan et al., 1978; Brush, 1983). Moreover, Serena (1981) and Cohan et al. (1978) reported that Bell's Vireo apparently discriminated against tamarisk for nesting purposes, possibly because of the sticky exudate which coated the shrub. Although tamarisk provided an inferior nesting resource on the lower Colorado River, it was reported to be of greater value to birds in other geographic areas including sections of the Pecos River and Rio Grande (Hunter et al., 1985).

Brown et al. (1983) attributed a range expansion and population increase for Bell's Vireo along the Colorado River in Grand Canyon to an increase in tamarisk-dominated habitat. Therefore, I examined the nest placement preferences of Bell's Vireo and several other riparian birds in that locale to help determine the role played by tamarisk in avian nest-site selection. The objective of the study was to test the null hypothesis that nest placement was random and that breeding birds did not show preference for tamarisk by nesting in it more often than in native shrubs. The frequency of nests in tamarisk should have approximately equalled the frequency of tamarisk shrubs near nest sites if nest placement was random. An important assumption of this test was that breeding passerines under study first chose a territory with suitable habitat attributes, and later selected appropriate vegetation for nest placement from within that territory.

I chose obligate riparian birds for study because they showed specialized habitat preferences by nesting only in riparian habitats in the Southwest (Johnson et al., 1977). Bell's Vireo, Yellow Warbler and Yellow-breasted Chat, the three most abundant obligate riparian passerines in the Grand Canyon section of the Colorado River, were the principal species examined. Additionally, adequate sample sizes of nests were obtained for three less common obligate riparian species: Willow Flycatcher, Common Yellowthroat, and Northern (Bullock's) Oriole.

Study Area

Study areas were established in the new-high-water-zone only. Primary study areas included Lees Ferry, Saddle Canyon, Cardenas Marsh, Lava Falls, Parashant Wash, and Granite Park.

Methods

Nests were located during the breeding seasons of 1982-84 by systematic ground searches of the riparian zone involving up to six observers. Numbers and species of shrubs were sampled in two perpendicular armlength transects (north to south, east to west) through the center of 0.04 ha circles centered at nests (James and Shugart, 1970). Shrubs were defined as woody vegetation >1.5 m in height. Expected values for numbers of nests per species were computed from the observed proportions of tamarisk to native shrubs. A chi-square goodness-of-fit test was used to examine the null hypothesis that nest placement in any given species of shrub was random.

Results and Discussion

Ninety-five of 105 nests sampled were located in tamarisk (See Table 15). The ten nests placed in native vegetation were: two Bell's Vireo nests and one Yellow-breasted Chat nest in arrowweed; two Common Yellowthroat nests in Goodding willow; one Bell's Vireo nest and two Yellow-breasted Chat nests in seepwillow; and two Common Yellowthroat nests in grasses and herbs (*Imperata brevifolia* and *Equisetum* sp.). The frequency of tamarisk at nest sites was variable, with the median frequency above 0.4 for all species except Common Yellowthroat (See Figure 3).

The null hypothesis of random nest placement was rejected for five of the six species of passerines. Willow Flycatcher, Bell's Vireo, Yellow Warbler, Common Yellowthroat, and Yellow-breasted Chat showed a significant preference for tamarisk over native vegetation (See Table 15). A highly significant preference for tamarisk was exhibited by the four species with the smallest median frequency of tamarisk in their nesting habitat (See Figure 3). Northern (Bullock's) Oriole did not show a statistical preference for tamarisk because of similarity between the expected and observed values of nest placement. However, Northern (Bullock's) Oriole exhibited an affinity for tamarisk because all oriole nests sampled were located in tamarisk (See Table 15) and because of the high proportion of tamarisk in oriole nesting habitat (See Figure 3).

The preference shown for tamarisk as a nest substrate by riparian birds in this study indicated that tamarisk was of more value to

Table 15. Observed and expected values for numbers of nests of riparian passerines nesting in tamarisk or in native vegetation along the Colorado River in Grand Canyon, 1982-84. P-values from a chi-square goodness-of-fit test are indicated for each species.

Species	No. of Nests in Tamarisk		No. of Nests in Native Plants		P-Value (1-sided)
	Observed	Expected	Observed	Expected	
Willow Flycatcher	8	5.1	0	2.9	.0160
Bell's Vireo	30	16.3	3	16.7	.0001
Yellow Warbler	19	11.5	0	7.6	.0002
Common Yellowthroat	11	5.1	4	9.9	.0006
Yellow-breasted Chat	16	11.9	3	7.0	.0006
Northern Oriole	11	10.1	0	0.9	.1590
Total	95	60.0	10	45.0	

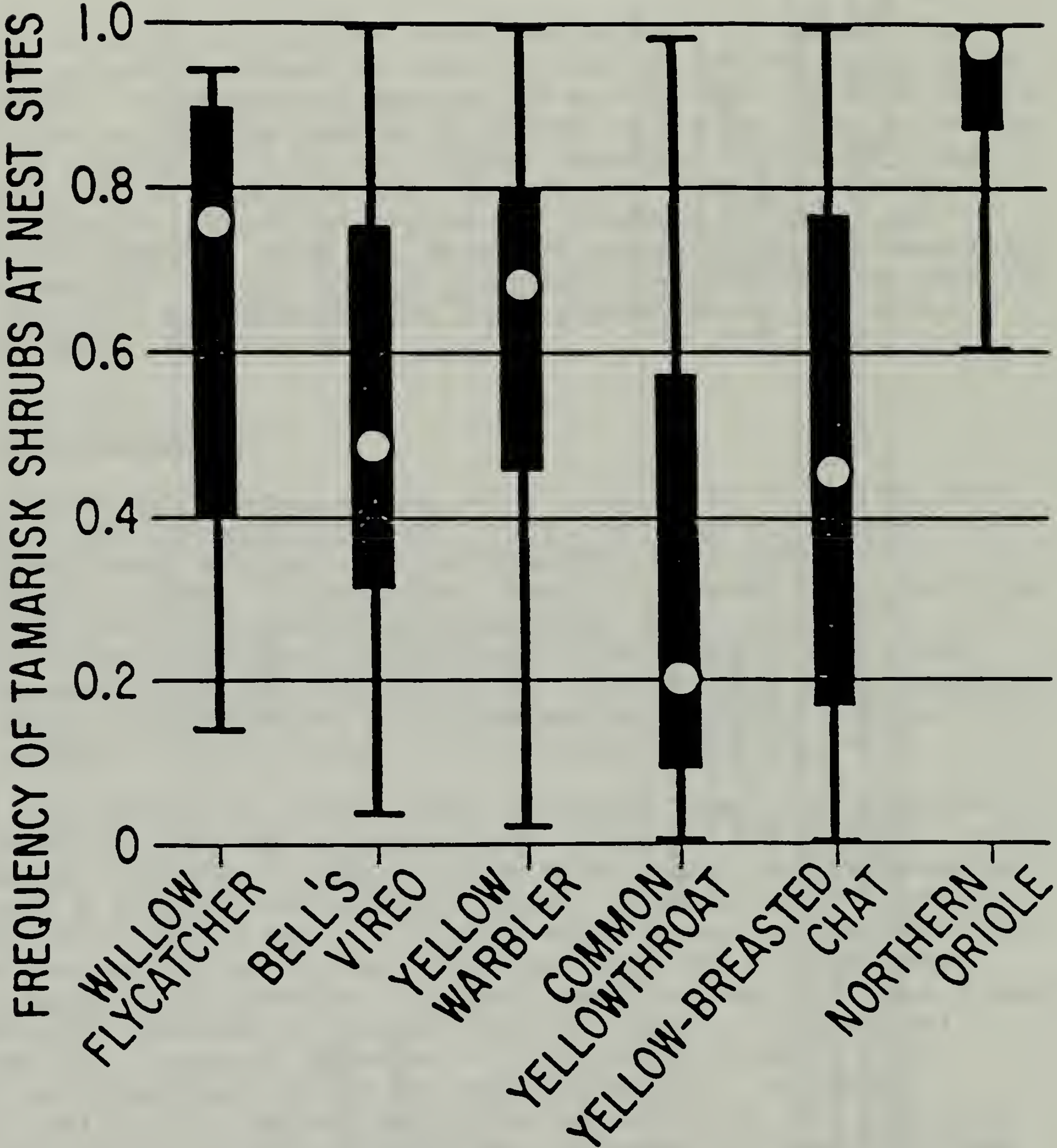

Figure 3. Range (brackets), interquartile range (bold lines), and median (circle) of frequencies of tamarisk shrubs at nest sites of riparian passerines along the Colorado River in Grand Canyon National Park, Arizona, 1982-85.

breeding birds as a nest substrate plant than had been shown by previous studies. This study did not address nest-site selection in riparian systems without tamarisk, and different results would be expected from those areas. However, most low-elevation riparian areas of the southwestern deserts, especially those in the Colorado River drainage, have been invaded by tamarisk to some extent. If tamarisk is of more value to breeding birds than native riparian shrubs in some geographic areas, then the management of tamarisk as avian nesting habitat should vary on a regional basis. The comparisons made in this study supported the contention of Hunter et al. (1985) that the usefulness of tamarisk habitats to birds was subject to geographic variation.

REFERENCES CITED

Anderson, B. W., A. Higgins, and R. D. Ohmart. 1977. Avian use of saltcedar communities in the Lower Colorado River Valley. Pp. 128-136 in R. R. Johnson and D. A. Jones (tech. coord.), Importance, preservation, and management of riparian habitats. A symposium. USDA For. Serv. Gen. Tech. Rep. RM-43.

Austin, G. T. 1970. Breeding birds of desert riparian habitat in southern Nevada. Condor 72:431-436.

Brown, B. T., S. W. Carothers, and R. R. Johnson. 1983. Breeding range expansion of Bell's Vireo in Grand Canyon, Arizona. Condor 85:499-500.

Brush, T. 1983. First nesting of a New World woodpecker in tamarisk (Tamarix chinensis). Southwest. Nat. 28:113.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. J. Forestry 39:388-394.

Carothers, S. W., R. R. Johnson, and S. W. Aitchison. 1974. Population structure and social organization of southwestern riparian birds. Amer. Zool. 14:97-108.

Cohan, D. R., B. W. Anderson, and R. D. Ohmart. 1978. Avian population responses to salt cedar along the Lower Colorado River. Pp. 371-382 in R. R. Johnson and J. F. McCormick (tech. coord.), Strategies for the protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12.

Collins, S.L. 1981. A comparison of nest-site and perch- site vegetative structure for seven species of warblers. Wilson Bull. 93:542-547.

Conner, R. N., and C. S. Adkisson. 1977. Principal component analysis of woodpecker nesting habitat. Wilson Bull. 89:122-129.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323-342.

Gavin, T. A., and L. K. Sowls. 1975. Avian fauna of a San Pedro Valley mesquite forest. J. Arizona Acad. Sci. 10:33-41.

Gill, F. B., and L. L. Wolf. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333-345.

Gnanadesikan, R. 1977. Methods for statistical data analysis of multivariate observations. John Wiley and Sons, New York.

Horton, J. S. 1977. The development and perpetuation of the permanent tamarisk type in the phreatophyte zone of the Southwest. Pp. 124-127 in R.R. Johnson and D.A. Jones (tech. coor.), Importance, preservation, and management of riparian habitat: a symposium. USDA For. Serv. Gen. Tech. Rep. RM- 43.

Hunter, W.C., B.W. Anderson, and R.D. Ohmart. 1985. Summer avian community composition of Tamarix habitats in three southwestern desert riparian systems. p. 128-134 in R. R. Johnson et al. (tech. coor.), Riparian ecosystems and their management: reconciling conflicting uses. USDA For. Serv. Gen. Tech. Rep. RM-120.

James, F. 1971. Ordination of habitat relationships among breeding birds. Wilson Bull. 47:215-236.

James, F. 1978. On understanding quantitative surveys of vegetation. Amer. Birds 32:18-21.

James, F., and H. Shugart. 1970. A quantitative method of habitat description. Aud. Field Notes 24:727-736.

James, G.S. 1954. Tests of linear hypotheses in univariate and multivariate analysis when the ratios of the population variances are unknown. Biometrika 41:19-43.

Johnson, R. R. 1978. The Lower Colorado River: a western system. Pp. 41-55 in R. R. Johnson and J. F. McCormick (tech. coor.), Strategies for the protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12.

Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pp. 68-79 in R. R. Johnson and D. A. Jones (tech. coor.), Importance, preservation, and management of riparian habitat: a symposium. USDA For. Serv. Gen. Tech. Rep. RM-43.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacKenzie, D.I., and S.G. Sealy. 1981. Nest site selection in Eastern and Western Kingbirds: a multivariate approach. Condor 83:310-321.

MacKenzie, D.I., S.G. Sealy, and G.D. Sutherland. 1982. Nest-site characteristics in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. Can. J. Zool. 60:2212-2223.

Martinka, R.R. 1972. Structural characteristics of Blue Grouse territories in southwestern Montana. J. Wildl. Manage. 36:498-510.

Maurer, B.A., and R.C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structure. Wilson Bull. 93:478-490.

Mayfield, H. F. 1981. Problems in estimating population size through counts of singing males. Studies in Avian Biology 6:220-224.

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent. 1975. Statistical package for the social sciences. Second Ed. McGraw-Hill Book Co., New York.

Odum, E. P. 1959. Fundamentals of ecology. W. B. Saunders Co., Philadelphia, Pennsylvania.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

Raphael, M. G. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pp. 142-151 in D. Capen (tech. coord.), The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv. Gen. Tech. Rep. RM-87.

Rice, J., R. D. Ohmart, and B. W. Anderson. 1983. Habitat selection attributes of an avian community: a discriminant analysis investigation. Ecol. Monogr. 53:263-290.

Robinson, T. W. 1965. Introduction, spread, and areal extent of saltcedar (Tamarix) in the western states. USDI Geol. Survey Prof. Pap. 491-A, U.S. Govt. Print. Off., Washington, D.C.

Rosenberg, K. V., R. D. Ohmart, and B. W. Anderson. 1982. Community organization of riparian breeding birds: response to an annual resource peak. Auk 99:260-274.

Serena, M. 1981. Distribution, habitat preferences, and reproductive success of Arizona Bell's Vireo (Vireo bellii arizonae) along the Lower Colorado River. Nongame Wildl. Investigations, California Dept. of Fish and Game, Sacramento.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819.

Stamp, N. E. 1978. Breeding birds of riparian woodland in south-central Arizona. Condor 80:64-71.

Stevens, L. E. 1976. Insect production on native and introduced dominant plant species. Pp. 129-135 in S. W. Carothers and S. W. Aitchison (eds.), An ecological survey of the riparian zone of the Colorado River between Lees Ferry and Grand Wash Cliffs. Colorado River Tech. Rep. No. 10, Grand Canyon National Park, Grand Canyon, Arizona.

Stevens, L. E. 1983. The Colorado River in Grand Canyon: a comprehensive guide. Red Lake Books, Flagstaff, Arizona.

Szaro, R. C., and M. D. Jakle. 1982. Comparison of variable circular-plot and spot-map methods in desert riparian and scrub habitats. Wilson Bull. 94:546-550.

Turner, R. M., and M. M. Karpiscak. 1980. Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. USDI Geol. Survey Prof. Pap. 1132, U. S. Govt. Print. Off., Washington, D. C.

Whitmore, R.C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

Whitmore, R.C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253-265.

Willet, T., and A.C. Van Velzen. 1984. Forty-seventh breeding bird census. Amer. Birds 38:64-129

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.